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Do multipurpose companion trees affect high value timber trees in a silvopastoral plantation system?

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Abstract Establishment of native timber trees on deforested land may contribute to the livelihood of farmers, to improved ecosystem services and to increased greenhouse gas uptake. Here, we present a new silvopastoral planting design to assess species performance and interspecific competition or facilitation effects among native timber and multipurpose trees in Central America. Two timber species, *Tabebuia rosea* and *Cedrela odorata*, were established in three low-density planting regimes allowing combined tree and future livestock production: (1) solitary planting, (2) companion planting with *Guazuma ulmifolia*, and (3) companion planting with the nitrogen-fixing *Gliricidia sepium*. We quantified survival, growth and reforestation potential of the two timber species subjected to the different planting regimes for the first 2 years after establishment. Nitrogen concentration as well as stable nitrogen and carbon isotope composition (δ^{15}N, δ^{13}C) of leaves of the timber saplings were determined. *T. rosea* showed higher survival and better growth than *C. odorata* under varying environmental conditions (soil, concomitant vegetation). Performance of the timber saplings was unaffected by either companion species. Planting regimes had no effect on foliar nitrogen concentration and δ^{15}N of the two timber species, although δ^{15}N values indicated nitrogen fixation activity in *G. sepium* trees. Planting regimes affected foliar δ^{13}C values in *T. rosea*. δ^{13}C values were significantly higher in solitarily growing individuals, suggesting lower exposition to water stress conditions in saplings surrounded by companion species. As we found positively correlated growth traits among timber and multipurpose trees, a combined planting may benefit farmers by providing additional goods and services.

Keywords *Cedrela odorata* · Multipurpose companion trees · REDD · Silvopastoral systems · *Tabebuia rosea* · Timber tree performance

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Introduction

Afforestation and reforestation are considered to an increasing degree as a development tool for the rural poor in many Latin American countries (Nelson and

De Jong 2003; Tschakert et al. 2007). Currently plantations are eligible for carbon credits under the Clean Development Mechanism of the Protocol of Kyoto, and they may become part of a new mechanism being developed under the United Nations Framework Convention on Climate Change known as REDD+ (reducing emissions from deforestation and forest degradation in developing countries), provided that they are used as tools to reduce deforestation. The inclusion of plantations in a REDD+ mechanism is supported by countries such as New Zealand (C. Potvin, pers. obs.), whereas other countries see plantations as a threat to biodiversity (Danielsen et al. 2008). As planting trees in degraded tropical landscapes can have positive effects on soil conditions and the regeneration of woody species (Haggar et al. 1998; Jones et al. 2004; Lugo 1997; Montagnini 2001; Nichols et al. 2001; Sierra et al. 2002), tree establishment may mitigate or reverse the negative impacts of land degradation in the tropics.

Plantation forestry in Latin America has traditionally concentrated on a few well-known exotic species, primarily established in monocultures representing over 99% of the tree plantations in this region (Evans and Turnbull 2004). Well-managed monoculture plantations of exotic tree species may be productive under favorable conditions, but these species have often been selected to produce a very limited set of goods and services and may decrease plant biodiversity (Healy et al. 2008; Kanowski et al. 2005), reduce soil quality (Lugo 1997) and promote soil erosion (Lamb et al. 2005; Wishnie et al. 2007). Using native species may have several advantages (Garen et al. 2009; Keenan et al. 1999), as these species (1) are already adapted to their native habitats, (2) may show more positive effects on local biodiversity and ecosystem processes, (3) can be grown from naturally available seeds, which reduces the dependency on external seed sources and foreign technologies and lowers economical investments, (4) have the potential to fulfill a wide range of landholder needs, and (5) might reduce deforestation pressure on remnant natural forests providing traditionally used non-timber products to the rural population. More than 100 tree species native to Panama are already used regularly as timber, fuel wood, fodder and for other products (Aguilar and Condit 2001; Haggar et al. 1998; Love and Spaner 2005; Wishnie et al. 2007). Nevertheless, planting native tree species is perceived by local farmers as a high-risk activity because of the paucity of data on the performance of native species in newly established tree plantations on degraded pastures (Garen et al. 2009), and only little scientific support to ensure economic success is available so far (Dagang and Nair 2003). Furthermore, tree plantations do not provide short-term economical benefit, which increases the need for land use types allowing for coexistence of trees and cattle as dominant rural economy in Latin America (Garen et al. 2009).

Silvopastoral systems, a combination of timber, fuelwood or fruit trees with animals, are considered to be a promising option to bring back selected useful trees to current extensive pastures. The incorporation of multipurpose trees on grassland may represent a promising strategy to combat erosion and desertification (Danso et al. 1992), to provide shading trees for cattle, and pest control for crops or high-value timber trees (Bellow and Nair 2003; Navarro et al. 2004; Rowe et al. 2005; Wagner et al. 1996), to contribute additional income and diversified goods and services required by landholders, and to improve land-use efficiency by providing livestock nutrition in the dry season (Dagang and Nair 2003; Garen et al. 2009; Love and Spaner 2005; Love et al. 2009; Montagnini and Jordan 2005; Wishnie et al. 2007). Integration of nitrogen fixing trees into these silvopastoral systems may improve land use by restoring and maintaining soil fertility and consequently facilitating nitrogen availability for adjacent crops (Nygren and Leblanc 2009) or grasses of surrounding pastures (Daudin and Sierra 2008; Jayasundara et al. 1997; Sierra and Nygren 2006).

Successful management of silvopastoral systems requires knowledge on suitable species and site attributes and a profound understanding of their interactions. Species-specific responses to competition, competitive reduction and facilitation effects can be regarded as dominating factors influencing survival, productivity and overall yield of trees within the first years after establishment (Forrester et al. 2006; Jose et al. 2006; Kelty 2006). Although rarely tested experimentally, initial spacing of trees and varying neighborhood-effects affected by either nitrogen-fixing or non-nitrogen-fixing companion trees should have strong effects on the above-mentioned interactions during tree establishment (Grant et al. 2006; Potvin and Dutilleul 2009).

Here we present results from a study on the reforestation potential of two native timber species from Central America in a newly developed planting design for silvopastoral systems on former pastures. Saplings were established at low density as solitary timber trees, or as a combination of timber trees with nitrogen-fixing or non-nitrogen-fixing multipurpose companion trees. The purpose of the study was (1) to compare the species-specific development of the timber species in a variable pasture-reforestation environment, and (2) to test how the different planting regimes influence the specific establishment-performance in survival, growth and reforestation potential of the timber trees. We hypothesized that (a) solitarily growing timber saplings exhibit a divergent survival and growth performance compared to those individuals surrounded by multipurpose companion tree species due to differing competitive conditions and varying microhabitats. We further hypothesized that (b) nitrogen-fixing companion species lead to a facilitation effect for the accompanied timber species due to increased N availability, resulting in an improved growth performance in comparison to solitarily growing individuals and those planted in combination with a non-nitrogen-fixing companion species.

Materials and methods

Study site and tree species

The experimental site is located in Central Panama, Province Colon, at Sardinilla (9°19′30″N, 79°38′00″W). The elevation is around 70 m a.s.l., mean annual precipitation is 2350 mm, with 25–50 mm per month during the dry season (January–April), and >250 mm mean monthly precipitation during the rainy season (May–December). Daily and seasonal temperatures are relatively constant throughout the year, with annual daily maximum temperatures of 33.1°C and an annual daily minimum of 21.7°C. The original semi-deciduous forest was logged in 1953, and after 2 years of cultivation converted into pasture to graze cattle for almost 50 years (Scherer-Lorenzen et al. 2007; Wilsey et al. 2002). The study was conducted during the first 2 years after tree establishment (year 1: 09/2006–08/2007, year 2: 09/2007–08/2008), with some additional measurements in the subsequent year (2009). Climatic conditions in the study period are characterized in the context of long-term average conditions (Table 1). Annual precipitation and number of dry days recorded in the two main study years are compared to the respective values of a base period from 1967 to 2005. During this base period, data for 35 of 38 years were available. Data were obtained from the Panama Canal Authority Meteorological Service weather station network (ACP 2009) for a weather station located at nearby Salamanca, 5 km from the Sardinilla study site.

Two timber species and two multipurpose companion species were selected based on their (1) forest restoration potential, (2) commercial importance on a regional, national and international scale, and (3) comparability with an already established improved afforestation system at the experimental site. All four species are native to the study region. They are planted to an increasing degree across Central America by forestry companies and farmers, because of their high value as timber or as traditional multipurpose trees (ACP 2005; Cajas-Giron and Sinclair 2001; Wishnie et al. 2007).

The timber species selected were *Tabebuia rosea* Bertol. (Bignoniaceae) and *Cedrela odorata* L. (Meliaceae). Under natural conditions, *T. rosea* can be found as isolated trees, in essentially pure stands, or in mixed forests (Longwood 1971). It has been used as an ornamental or shade tree and can also be found in commercial plantations (Pennington and Sarukhan 1968). *C. odorata* is a fast-growing, light demanding tree species. Under natural conditions, it is a long-lived pioneer that tolerates shade only temporarily (Carpenter et al. 2004). It is recommended to plant this timber species in regions

Table 1 Precipitation and number of dry days (without precipitation) at Salamanca weather station[a]

	Base period (mean ± SE)	Year 1	Year 2
Precipitation (mm)	2191.0 (±66.2)	2826.0	2963.0
Number of dry days	152.6 (±4.17)	176.0	175.0

[a] Data of the base period were derived for 35 preceding years from ACP (ACP 2009). They are given as mean value of the 12 months periods from September to August of a consecutive year that were also used for sapling growth measurements. Data of study year 1 (09/2006–08/2007) and study year 2 (09/2007–08/2008) are given as total values for the respective time slot

with very fertile soils and with perfect drainage providing a good aeration of the soil, which is required for efficient root development (AgroForestryTreeDatabase 2009).

The companion tree species selected were *Gliricidia sepium* (Jacq.) Kunth ex Walp. (Fabaceae) and *Guazuma ulmifolia* Lam. (Sterculiaceae). *G. sepium* is a widely adapted, fast-growing tree favored by farmers as erosion control and living fence as well as a versatile legume providing fuel wood, green manure and shade for livestock and crops. The crops may also benefit from the nitrogen-fixing properties of *G. sepium* (Danso et al. 1992; Graham and Vance 2003; Rowe et al. 2005). *G. ulmifolia* is a small to medium-size tree species developing best in full sunlight. The wood is used for traditional medicine, general carpentry, light construction and as fuel (Cajas-Giron and Sinclair 2001; Jiménez-Ferrer et al. 2008; Wishnie et al. 2007). Foliage of both companion tree species, *G. sepium* and *G. ulmifolia*, is an important source of feed supplement for livestock, particularly at the end of the dry season when pasture grasses are not available (Cajas-Giron and Sinclair 2001; Love and Spaner 2005).

Planting design

Experimental silvopastoral plots were established on former pasture at the Sardinilla site in August 2006. Potted seedlings of *T. rosea*, *C. odorata*, *G. sepium*, and *G. ulmifolia* were raised in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery for 3 months before being planted on the pasture. To support tree establishment, 15 g of 12–72–12 N–P–K granular fertilizer was applied to each seedling at the time of planting to the bottom of each planting hole and covered with soil before planting, and again 2 months after planting to each seedling on the soil surface.

Seedlings of the timber species *T. rosea* and *C. odorata* were planted at 9 m distance from one another in three different planting regimes: (1) solitarily, (2) accompanied by *G. sepium* or (3) accompanied by *G. ulmifolia*. In the two latter planting regimes, five companion seedlings of the same species were planted circularly around a central timber seedling at a distance of 1.5 m. Besides tree production, the silvopastoral plots can be used for future livestock grazing because of the relatively low density of timber trees. A silvopastoral plot comprised both timber species, planted in each of the three planting regimes in a random arrangement, and each planting regime was based on eight timber tree individuals, resulting in 48 timber trees per plot (94 timber trees per hectare). Three silvopastoral plots varying in slope and aspect were established at different locations of the Sardinilla site. After planting, competing vegetation in the plots was cleared with machetes every 3 months during the rainy season shortly before the measurements of sapling growth.

Plot characterization

To quantify environmental variation among the silvopastoral plots, chemical and physical soil properties as well as biomass of herbaceous vegetation were determined in May 2009. Soil was sampled from 12 uniformly distributed locations across each plot. Samples were taken from 0–5 cm, 5–10 cm and 15–20 cm soil depth using a cylindric corer. They were dried at 65°C to weight constancy before quantification of pH, N, and C concentration. Soil pH was determined in soil water solution according to NF ISO 10390 (2005) using a Metrohm 780 pH meter (Metrohm Schweiz AG, Zofingen, Switzerland). Analyses of total N and C concentration were conducted using a Flash EA 1112 Series elemental analyser (Thermo Italy, Rhodano, Italy). Soil moisture was measured as the proportion of water per soil sample, calculated from the weight before and after drying.

Aboveground herbaceous vegetation was sampled in square grids (0.5 × 0.5 m) from 8 locations that were uniformly distributed across each plot. Vegetation within the grids was clipped to ground level, sorted for living and dead plant material and dried at 65°C to weight constancy before determination of dry biomass.

Tree survival and growth

Survival and sapling growth of the timber species *T. rosea* and *C. odorata* were quantified on an annual basis over 2 years, i.e. from August 2006 until August 2008. As indicators of tree growth, total height (taken from the uppermost point in the tree crown to the soil) and basal stem diameter (diameter at 10 cm above soil surface) of all timber saplings were measured. To assess the potential impact of

companion tree growth on the timber species *T. rosea* and *C. odorata*, total tree height, canopy height (distance from the lowest branch to the uppermost point in the tree crown), cross sectional area of the canopy (calculated as an ellipse from maximum perpendicular diameters), and total leaf number were determined for the companion species *G. sepium* and *G. ulmifolia* 1 and 2 years after establishment.

Nitrogen and carbon analyses in leaves

The effects of planting regimes on nitrogen availability and drought stress for the timber species were assessed by C–N elementary and stable isotope analysis. A representative sample of at least four mature leaves was haphazardly collected from each central timber sapling and dried at 60°C to weight constancy. All leaves collected per tree were then milled to a homogenized powder using a Retsch ball mill MM200 (Retsch GmbH, Haan, Germany). Leaf powder was used to quantify for each tree (1) total nitrogen concentration of mature leaves, (2) the δ^{15}N ratio in mature leaves to test for a possible nitrogen provision by the surrounding nitrogen fixing *G. sepium* (Daudin and Sierra 2008; Nygren and Leblanc 2009), and (3) the δ^{13}C values of mature leaves as a measure of plant stress (Farquhar et al. 1989; Mody et al. 2009). To test nitrogen fixation activity in *G. sepium*, mature leaves were sampled for each of the five companion individuals surrounding one single timber sapling. Stable isotope analyses were carried out for the combined samples of the five *G. sepium* individuals.

Analyses of isotope proportion and nitrogen concentration were conducted using a Flash EA 1112 Series elemental analyzer (Thermo Italy, Rhodano, Italy) coupled to a Finnigan MAT Delta plus XP isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) via a six-port valve and a ConFlo III. The positioning of samples, blanks and (laboratory) standards (Identical-Treatment principle) in a measurement series for the carbon isotope ratio measurements, followed the procedure described by Werner and Brand (2001). Post-run off-line calculations like blank-, offset- and possibly drift-corrections for assigning the final δ-values on the V-PDB scale were performed according to Werner and Brand (2001).

To identify whether the companion tree *G. sepium* exhibited any nitrogen-fixing activity, δ^{15}N values were plotted against nitrogen concentration. Generally, aerial N_2-fixing activity in legume species is characterized by high N concentrations and low δ^{15}N values. In contrast, non-legume species show lower N concentrations with higher δ^{15}N values. Such divergent characteristics between the two groups, together with a δ^{15}N signal from a legume plant close to 0 ‰, are considered to be a clear indication that the investigated legume was actively fixing nitrogen (Temperton et al. 2007).

Statistical analyses

Prior to analysis, data were transformed where necessary to meet the assumptions of normality and heteroscedasticity for parametric tests. Plot characteristics were arcsin-transformed (soil C and N, soil moisture) or log-transformed (soil pH, biomass, vegetation height). Growth measurement values were log-transformed, and leaf nitrogen concentration was arcsin-transformed.

Comparisons of soil properties were conducted using two-way repeated measures ANOVA, with soil depth as within-subject repeated factor and silvopastoral plot as between-subject factor. Biomass of herbaceous vegetation in the silvopastoral plots was compared by one-way ANOVA. Mortality was compared for the two timber species, and for the three planting regimes for each species using contingency chi-square tests. Analyzes of tree growth traits were conducted for values measured 2 years after establishment. Effects of planting regimes on timber sapling growth were assessed by two-way ANOVA, with treatment and plot as fixed factors. Growth traits of *G. sepium* and *G. ulmifolia* were analyzed using the mean value of the five individuals surrounding a single timber sapling. Pearson correlation analyses revealed strong correlations between tree height and the growth traits canopy height, canopy diameter and total leaf number (*G. sepium*: $r = 0.842$ to $r = 0.995$, and $r = 0.741$ to $r = 0.985$, for the first and the second year, respectively; *G. ulmifolia*: $r = 0.943$ to $r = 0.993$ and $r = 0.901$ to $r = 0.942$, for the first and the second year, respectively). Therefore, all analyses referring to companion tree growth were restricted to the growth trait 'height' for the second

year. Height of companion species in different plots was compared using a one-way ANOVA with plot as fixed factor. Comparisons between planting regimes and single plots were only conducted for *T. rosea* because of low survival and resulting reduced individual numbers of *C. odorata*. Effects of planting regimes on C–N-values of timber species leaves were assessed by two-way ANOVA, with treatment and plot as between-subject factors. For multiple comparisons in ANOVA analyses, LSD post hoc tests were applied.

All statistical analyses were conducted with SPSS 16.0 for Mac OS X (2007; SPSS, Chicago, IL, USA). For clarity, all figures show untransformed data.

Results

Plot characterization

The three silvopastoral plots (SP1-SP3) differed significantly in nitrogen concentration and soil moisture (Table 2). Soil nitrogen concentration was significantly higher in SP1 than in SP3. Soil moisture was significantly lower in SP1 than in SP3. Soil characteristics changed also significantly with soil depth (Table 2). Soil nitrogen and carbon concentration were consistently highest in the 5 cm surface layer and lowest in the deepest level at 20 cm. Soil pH was significantly higher at a depth of 20 cm than at 5 cm or 10 cm (Table 2). Both living and dead herbaceous biomass as well as vegetation height were significantly lower in SP1 than in SP2 and SP3.

Tree survival and growth

Survival differed significantly among timber species ($\chi^2 = 4.06$, $P < 0.001$) but it was not significantly affected by planting regime for neither *Tabebuia rosea* nor *Cedrela odorata* (*T. rosea*: $\chi^2_{(2)} = 0.53, P = 0.77$; *C. odorata*: $\chi^2_{(2)} = 1.00, P = 0.60$) (Fig. 1). Mortality in *T. rosea* was very low (5.6%, $n = 4$). In contrast, *C. odorata* showed high mortality with more than half of all planted individuals (54.2%, $n = 39$) dying within the first 2 years after planting. Tree death was completely (*T. rosea*) or largely (*C. odorata*) restricted to the first year after establishment.

Two years after establishment, sapling height and stem diameter were generally higher in *T. rosea* than in *C. odorata*, perceivable in the higher mean values of the measured growth traits (*t*-tests; height: $t = -9.77$, $P < 0.001$; stem diameter: $t = -6.56$, $P < 0.001$) (Table 3). Planting regimes had no effect on height and basal stem diameter of *T. rosea* (height: $F_{2,59} = 0.26$, $P = 0.774$; diameter: $F_{2,59} = 0.30$, $P = 0.740$). No significant planting regime × plot interaction was found for the two growth traits, but plot effect was strong for height of *T. rosea* saplings. Height varied significantly among plots, with saplings growing in SP3 being significantly higher than those growing in SP1 and SP2 ($F_{2,59} = 4.62$, $P = 0.014$; $P_{SP3/SP2} = 0.005$; $P_{SP3/SP1} = 0.024$; $P_{SP2/SP1} = 0.512$; $\bar{h}_{SP3} = 205.6 \pm 18.9$ cm, $\bar{h}_{SP2} = 131.9 \pm 13.3$ cm, $\bar{h}_{SP1} = 146.4 \pm 12.1$ cm). No significant differences in stem diameter were found ($F_{2,59} = 2.29$, $P = 0.110$), although saplings in SP3 tended to have a larger diameter than saplings in SP2 ($\bar{d}_{SP3} = 36.5 \pm 3.4$ mm, $\bar{d}_{SP1} = 30.1 \pm 2.5$ mm, $\bar{d}_{SP2} = 25.6 \pm 1.9$ mm).

In *C. odorata*, low survival and the resulting reduced individual numbers disallowed comparisons of growth traits between planting regimes and single plots. However, variation in sapling height and basal stem diameter between planting regimes appeared to be relatively low for both years (Table 3).

In the companion species *Gliricidia sepium*, sapling height was significantly different among the three plots 2 years after establishment ($F_{2,45} = 3.94$, $P = 0.027$). Saplings in SP3 grew higher than those planted in SP1, and also individuals in SP2 tended to achieve greater heights than those planted in SP1 ($P_{SP3/SP1} = 0.009$; $P_{SP2/SP1} = 0.068$; $P_{SP3/SP2} = 0.385$; $\bar{h}_{SP3} = 320.3 \pm 27.4$ cm, $\bar{h}_{SP2} = 286.4 \pm 28.6$ cm, $\bar{h}_{SP1} = 230.7 \pm 24.8$ cm). In the companion species *Guazuma ulmifolia*, growth performance significantly differed among all three plots 2 years after establishment ($F_{2,45} = 19.40$, $P < 0.001$, $P_{SP1/SP2} = 0.015$; $P_{SP1/SP3} = 0.004$; $P_{SP2/SP3} < 0.001$). Saplings grew highest in SP3 ($\bar{h}_{SP3} = 420.3 \pm 47.4$ cm), followed by SP1 ($\bar{h}_{SP1} = 224.9 \pm 20.1$ cm) and SP2 ($\bar{h}_{SP2} = 149.4 \pm 16.6$ cm).

Growth traits of *T. rosea* were significantly positively correlated with growth traits of surrounding *G. ulmifolia* (height: $r = 0.591$, $P = 0.003$; stem diameter: $r = 0.454$, $P = 0.029$). No correlation was found between *T. rosea* and *G. sepium*. Growth traits of *C. odorata* were also significantly positively correlated with those of *G. ulmifolia* (height: $r = 0.868$, $P = 0.001$; stem diameter: $r = 0.673$,

Table 2 Soil and vegetation characteristics (mean ± SE) of the three silvopastoral plots (SP). Contrasting letters a,b,c refer to significant differences between plots or soil depths (D1 = 0–5 cm, D2 = 5–10 cm, D3 = 15–20 cm) for the specific characteristic[a]

Characteristic		SP1	SP2	SP3	ANOVA
Soil	Soil depth				
Nitrogen concentration (%)	D1	0.67 (±0.03)	0.55 (±0.03)	0.52 (±0.02)	Plot: $F_{2,33} = 5.35$, $P = 0.01$; $SP1^a > SP3^b$; $SP2^{ab}$
	D2	0.34 (±0.03)	0.38 (±0.02)	0.30 (±0.01)	
	D3	0.21 (±0.02)	0.25 (±0.02)	0.19 (±0.01)	Depth: $F_{2,66} = 272.70$, $P < 0.001$; $D1^a > D2^b > D3^c$
Carbon concentration (%)	D1	7.32 (±0.34)	6.24 (±0.33)	6.19 (±0.28)	Plot: $F_{2,33} = 2.30$, $P = 0.116$;
	D2	3.98 (±0.32)	4.40 (±0.26)	3.69 (±0.16)	Depth: $F_{2,66} = 307.08$, $P < 0.001$; $D1^a > D2^b > D3^c$
	D3	2.61 (±0.20)	2.96 (±0.25)	2.37 (±0.09)	
Moisture (%)	D1	27.5 (±1.0)	31.4 (±2.8)	31.3 (±1.1)	Plot: $F_{2,33} = 3.74$, $P = 0.034$; $SP3^a > SP1^b$; $SP2^{ab}$
	D2	26.4 (±1.0)	30.8 (±2.3)	30.9 (±0.9)	
	D3	29.9 (±0.4)	30.4 (±0.4)	32.6 (±0.4)	Depth: $F_{2,66} = 1.83$, $P = 0.168$;
pH	D1	5.30 (±0.11)	5.19 (±0.11)	5.41 (±0.08)	Plot: $F_{2,33} = 1.75$, $P = 0.189$
	D2	5.29 (±0.05)	5.23 (±0.14)	5.45 (±0.1)	Depth: $F_{1.2,40.6} = 4.06$, $P < 0.043$; $D3^a > D1^b$, $D2^b$
	D3	5.46 (±0.11)	5.28 (±0.21)	5.62 (±0.1)	
Vegetation					
Biomass alive (g)	–	81.14 (±14.83)	244.75 (±62.41)	410.44 (±111.18)	Plot: $F_{2,22} = 11.40$, $P < 0.001$ $SP1^b < SP2^a$, $SP3^a$
Biomass dead (g)	–	78.5 (±19.38)	198.63 (±41.24)	224.5 (±36.65)	Plot: $F_{2,22} = 7.34$, $P = 0.004$ $SP1^b < SP2^a$, $SP3^a$
Height (cm)	–	7.86 (±1.01)	37.5 (±0.94)	58.75 (±14.07)	Plot: $F_{2,22} = 37.76$, $P < 0.001$ $SP1^b < SP2^a$, $SP3^a$

[a] Analysis of soil characteristics was carried out with two-way repeated measures ANOVA; vegetation characteristics were analyzed by one-way ANOVA; LSD *post hoc* test, $P < 0.05$

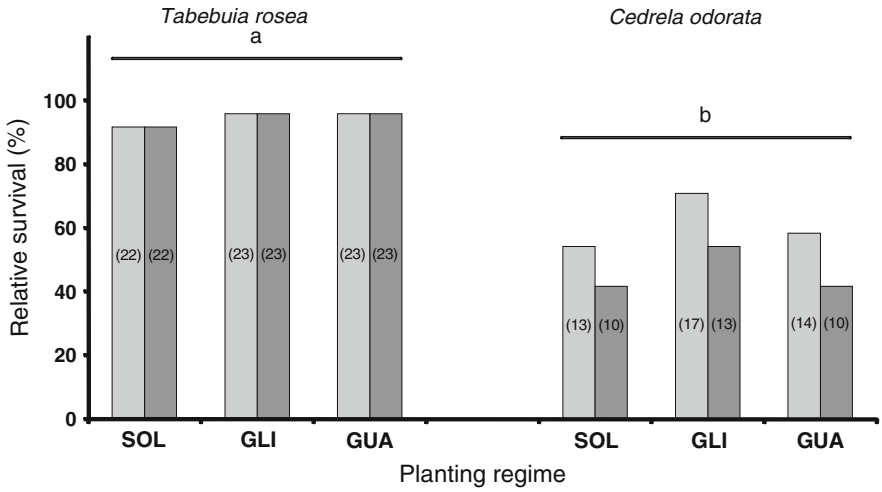

Fig. 1 Relative survival of the timber species *Tabebuia rosea* and *Cedrela odorata* 1 year (light grey bars) and 2 years (dark grey bars) after establishment. *T. rosea* and *C. odorata* were planted either solitarily (SOL), or accompanied by *Gliricidia sepium* (GLI) or by *Guazuma ulmifolia* (GUA). Absolute numbers of living trees are given in brackets. Contrasting letters refer to significant differences between species in total relative survival in all three treatments (χ^2-test, $P < 0.05$)

Table 3 Sapling growth traits (mean ± SE) 'height' (cm) and 'basal stem diameter' (mm) of *Tabebuia rosea* and *Cedrela odorata* individuals two years after planting. Both species were planted either solitarily (SOL), surrounded by *Gliricidia sepium* (GLI), or surrounded by *Guazuma ulmifolia* (GUA)

	Tabebuia rosea			*Cedrela odorata*		
	SOL	GLI	GUA	SOL	GLI	GUA
Height	163.6 (±17.3)	150.8 (±15.2)	168.3 (±16.5)	56.1 (±12.5)	57.9 (±16.9)	57.0 (±13.4)
Basal stem diameter	31.1 (±2.5)	29.6 (±3.0)	31.5 (±2.8)	16.7 (±4.6)	15.7 (±3.3)	16.8 (±4.1)

$P = 0.033$). Saplings of *C. odorata* surrounded by *G. sepium* showed positive correlations with the companion trees in height growth ($r = 0.552$, $P = 0.05$), but not for stem diameter ($P > 0.05$).

Nitrogen and carbon analyses in leaves

Nitrogen concentration was significantly higher in *T. rosea* leaves than in *C. odorata* leaves (*t-test*: $t = -3.72$, $P < 0.001$) (Table 4). δ^{15}N values were highly variable in both timber species in all three planting regimes (Table 4, Fig. 2), and they showed no significant differences among the two species (*t*-test: $t = 0.291$, $P = 0.771$). The three planting regimes had no significant impact on nitrogen concentration and δ^{15}N mean values in *T. rosea* leaves ($F_{2,59} = 2.34$, $P = 0.105$, and $F_{2,59} = 0.001$, $P = 0.999$, respectively).

No difference in the relationship between N concentrations and δ^{15}N values associated to the single planting regimes occurred in *T. rosea* and *G. sepium* leaves (Fig. 2). N concentrations in the leaves of the surrounding *G. sepium* individuals were significantly higher than N concentrations in leaves of both *T. rosea* (*t*-test: $t = -21.40$, $P < 0.001$) and *C. odorata* (*t*-test: $t = -18.09$, $P < 0.001$).

Mean δ^{13}C in *T. rosea* (-30.8 ± 0.12) was significantly higher than in *C. odorata* (*t-test*: $t = 9.54$, $P < 0.001$), in which δ^{13}C showed very low mean values (-32.9 ± 0.17). The three planting regimes affected the δ^{13}C values in *T. rosea* ($F_{2,59} = 6.34$, $P = 0.003$; Table 4). They were significantly higher in solitarily growing *T. rosea* individuals than in those surrounded by the companion species *G. sepium* or *G. ulmifolia* ($P_{SOL/GLI} = 0.011$; $P_{SOL/GUA} = 0.017$; $P_{GLI/GUA} = 0.985$).

A significant plot effect was observed in *T. rosea* for all three traits nitrogen concentration, δ^{15}N and δ^{13}C (N: $F_{2,59} = 9.20$, $P < 0.001$; δ^{15}N: $F_{2,59} = 8.72$, $P < 0.001$; δ^{13}C: $F_{2,59} = 5.79$, $P = 0.005$). Mean N concentration was significantly higher for saplings growing in SP3 ($N_{SP3} = 1.87 \pm 0.09\%$) than for those in SP1 and SP2 ($N_{SP1} = 1.48 \pm 0.05\%$ and $N_{SP2} = 1.51 \pm 0.06\%$; $P_{SP3/SP2} = 0.001$; $P_{SP3/SP1} < 0.001$; $P_{SP2/SP1} = 0.945$), whereas δ^{15}N values were significantly lower for saplings growing in SP1 ($\delta^{15}N_{SP1} = -0.11 \pm 19$) compared to SP2 and SP3 ($\delta^{15}N_{SP2} = 0.90 \pm 0.21$, and $\delta^{15}N_{SP3} = 1.20 \pm 0.28$; $P_{SP1/SP2} = 0.003$; $P_{SP1/SP3} < 0.001$; $P_{SP2/SP3} = 0.391$). δ^{13}C values in *T. rosea* were significantly higher in saplings growing in SP2 ($\delta^{13}C_{SP2} = -30.33 \pm 0.19$) than in SP1 and SP3 ($\delta^{13}C_{SP1} = -31.10 \pm 0.16$ and $\delta^{13}C_{SP3} = -30.83 \pm 0.24$; $P_{SP2/SP1} = 0.002$; $P_{SP2/SP3} = 0.045$; $P_{SP1/SP3} = 0.253$).

Table 4 Nitrogen concentration, δ^{15}N and δ^{13}C (mean ± SE) in mature leaves of *Tabebuia rosea* and *Cedrela odorata* 2 years after establishment. Both species were planted either solitarily (SOL), or accompanied by *Gliricidia sepium* (GLI), or by *Guazuma ulmifolia* (GUA)

	Planting regime		
	SOL	GLI	GUA
Tabebuia rosea			
N conc.	1.57 (±0.08)	1.72 (±0.07)	1.54 (±0.09)
δ^{15}N	0.63 (±0.24)	0.63 (±0.24)	0.66 (±0.29)
δ^{13}C	−30.28 (±0.24)	−31.01 (±0.15)	−30.97 (±0.19)
Cedrela odorata			
N conc.	1.20 (±0.13)	1.36 (±0.24)	1.33 (±0.18)
δ^{15}N	0.07 (±0.29)	0.35 (±0.39)	0.16 (±0.60)
δ^{13}C	−32.66 (±0.40)	−32.75 (±0.21)	−33.28 (±0.12)

Discussion

Effect of planting regimes

Survival and growth performance of the timber species *Tabebuia rosea* and *Cedrela odorata* were

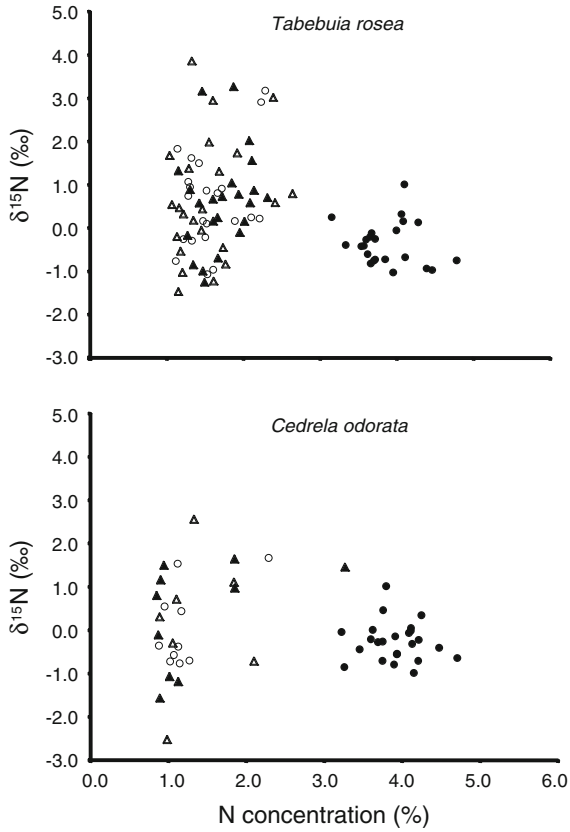

Fig. 2 Relationship between N concentration (%) and δ^{15}N values in mature leaves of the timber species *Tabebuia rosea* and *Cedrela odorata*. Saplings were planted either solitarily (*open circle*), accompanied by *Guazuma ulmifolia* (*open triangle*), or accompanied by the nitrogen fixing legume *Gliricidia sepium* (*closed triangle*). The relationship between N concentration and δ^{15}N values in mature leaves of accompanying *G. sepium* is given with the respective timber tree individual (*closed circle*)

not different among planting regimes within the first 2 years after establishment. This finding indicates that supplemented planting with the companion species *Gliricidia sepium* or *Guazuma ulmifolia* had neither competitive nor facilitative effects on survival and growth performance of the timber species in the tree establishment phase. Above-ground environmental conditions defined by the different planting regimes apparently were of negligible influence on survival and growth of the timber species, as no differences in survival and growth were noted between solitary saplings fully exposed to sunlight and saplings surrounded and partly shaded by companion species.

Nitrogen measures of mature leaves of the two timber species were not affected by planting regimes 2 years after establishment. Nitrogen concentration and δ^{15}N values were not significantly different for individuals surrounded by nitrogen fixing *G. sepium*, for individuals surrounded by *G. ulmifolia* or for solitary individuals. This finding suggests that *G. sepium* companion trees were not providing fixed atmospheric nitrogen to neighboring timber trees. To understand whether undistinguishable δ^{15}N values of mature leaves between the planting regimes were a consequence of lacking nitrogen fixation in the newly planted *G. sepium* individuals, nitrogen fixation by *G. sepium* individuals was tested half a year after the quantification of leaf nitrogen of the timber saplings. Low δ^{15}N values close to 0 ‰, indicated nitrogen fixation activity of all *G. sepium* individuals (Temperton et al. 2007). We assume that *G. sepium* already initiated nitrogen fixation activity in earlier stages of establishment as *G. sepium* has been reported to show strong fixation of atmospheric nitrogen already in the first year after planting (Kadiata et al. 1996). Thus, *G. sepium* companion trees provided no facilitation effect to the neighboring timber saplings during the first 2 years after establishment. This finding from our experiment might be attributed to a lack of root exudation, lack of common mycorrhizal networks, or to missing nitrogen transfer via root-to-root contact between the timber species and the companion species *G. sepium* (Daudin and Sierra 2008; Wagner et al. 1996). A significant facilitation effect may develop over a longer period of time. The importance of the factor time to establish measurable tree-to-tree interactions including exchange of nitrogen is supported by ^{15}N labeling experiments in mixtures of *Eucalyptus x robusta* and nitrogen-fixing *Casuarina equisetifolia* or *Leucaena leucocephala* trees (Parrotta et al. 1996). In this study, *E. x robusta* started nitrogen-uptake from both nitrogen fixing species 2 years after plantation establishment.

The finding that numerous individuals of both timber species exhibited δ^{15}N values around 0 ‰ irrespective of planting regime indicates that an external input of atmospheric nitrogen may have been relevant in different parts of the experimental plots. If not related to *G. sepium* presence, this nitrogen supply is probably attributable to legumes in the herbaceous layer, which could have provided establishing tree saplings with additional nitrogen.

Considering the carbon metabolism in the timber species, solitarily growing *T. rosea* saplings exhibited significantly higher $\delta^{13}C$ values than *T. rosea* individuals accompanied by *G. ulmifolia* and *G. sepium*. This may indicate increased water stress due to a stronger exposition to sunlight and higher temperatures in solitary individuals than in individuals surrounded by companion species (Heaton 1999; Ma et al. 2005). If the observed variation in $\delta^{13}C$ values is an indicator of drought stress, one would expect drought stress effects on growth or herbivore-plant interactions in longer-term assessments (Ma et al. 2005; Mody et al. 2009). However, the observed response has to be interpreted with care as environmental factors as well as genotypic differences may result in intraspecific variability in $\delta^{13}C$ values of up to 4 ‰ (Heaton 1999).

Timber species performance and environmental heterogeneity

Survival of *T. rosea* was in line with data from nearby forests on Barro Colorado Island (Welden et al. 1991) and from newly established plantations at the same study site in Sardinilla (Potvin and Gotelli 2008), or it even outperformed survival reported from mixed plantation systems (Wishnie et al. 2002) by more than 30%. Survival of *C. odorata* in plantations and agroforestry systems generally appears to be highly variable, ranging from very low (11%) to moderately high values (75%), hence the sapling survival of 46% found in the current study fits well into the range reported (Menalled et al. 1998; Navarro et al. 2004; Piotto et al. 2004; Potvin and Gotelli 2008).

In our study, abiotic factors such as precipitation, drought and soil quality influencing below-ground conditions, likely affected *C. odorata* survival. First, climatic conditions during the establishment phase were probably suboptimal for establishment of this sensitive tree species because of a combination of drought and water excess conditions (Engelbrecht et al. 2007). Compared to long-term average precipitation patterns, the newly established saplings were exposed to a larger number of dry days, with precipitation confined to a shorter time span during the annual growth periods in study year 1 and 2. The latter aspect might have resulted in waterlogged soils with negative consequences on sapling establishment. Hence, the current study supports recommendations to plant *C. odorata* at sites with well-drained soils (AgroForestryTreeDatabase 2009). Second, planting of saplings during the rainy season was shifted for more than 6 weeks towards the subsequent dry season compared to a similar former study at the same site (Potvin and Gotelli 2008), resulting in a shortened period for development of an adequate root system before onset of adverse dry season conditions.

Besides survival, sapling growth can be influenced by site conditions. The Sardinilla experimental site, designed to explore biodiversity and ecosystem functioning, has been found to encompass a high heterogeneity in soil and drainage characteristics (Healy et al. 2008). Differing growth performance of the timber species at the same location, as reported by the current study and a previous study from the same site (Delagrange et al. 2008), may be related to small-scale variation in soil and water conditions. Plot characteristics appeared to be more homogenous (and probably more suitable) in the study of Delagrange et al. (2008), whereas the experimental plots in our study were found to be heterogeneous in terms of soil nitrogen, soil moisture, and concomitant vegetation.

Besides heterogeneity in site conditions, insect herbivores have the potential to reduce tree growth in tree plantations. Whereas no major herbivore pest is known for *T. rosea* (Flores and Marín 2003), *C. odorata* is highly susceptible to infestations by the mahogany shoot borer *Hypsipyla grandella* Zeller and seldom escapes its severe attacks (Navarro et al. 2004; Pérez-Salicrup and Esquivel 2008). Damage by *H. grandella* generally retards or impedes height growth of *C. odorata*, particularly in saplings and younger trees (Griffiths 2001; Pérez-Salicrup and Esquivel 2008; Sands and Murphy 2001; Taveras et al. 2004), and repeated attacks may even kill the trees (Newton et al. 1993). In our study system, we found no differences in *H. grandella* infestation of *C. odorata* saplings among planting regimes, and mortality was seemingly unrelated to infestation with *H. grandella* (M. Plath et al., unpublished data). The infestation rate was considerably lower (30% of surviving individuals 2 years after establishment) compared to recent studies reporting mean infestation of up to 78% (Pérez-Salicrup and Esquivel 2008) or even 94% (Newton et al. 1998). Although infestation by *H. grandella* was less prevalent than in other studies, we cannot exclude some effect of this insect herbivore on growth of *C. odorata* in our study plots.

T. rosea, *G. sepium* and *G. ulmifolia* varied in growth performance between plots, reflecting species-specific habitat requirements that have to be considered when establishing trees on deforested land. For example, both *T. rosea* and *G. ulmifolia* grew better in plot 3 than in plot 1 and plot 2, which might reflect similar site requirements. In fact, soil water content was higher in plot 3 compared to the plots 1 and 2 confirming the relevance of water-related soil conditions for sapling growth (Healy et al. 2008). Accessibility of nitrogen to plants may be determined by small-scale variation in soil characteristics including water content and also clay content, which was not quantified in our study (Boomer and Bedford 2008; Daudin and Sierra 2008). Such factors might have contributed to our finding that, contrary to expectation, best growth of different tree species (*T. rosea*, *G. ulmifolia*, *G. sepium*) and highest levels of leaf nitrogen were recorded in plot 3 with lowest soil nitrogen concentration. The evidence that tree growth is not directly related to soil nitrogen concentration is also supported by findings obtained in another experimental plantation in the region, which is characterized by lower soil nitrogen concentrations under comparable climatic conditions (Wishnie et al. 2007). In that study, growth of *C. odorata* and *T. rosea* saplings, established few years prior to our study, exceeded growth traits measured in the present study after a 2 years growing period.

Although *T. rosea* exhibited differing sapling heights among the three plots, it constantly outperformed *C. odorata* in both growth performance and survival. *T. rosea* thus appears to be a more suitable timber species than *C. odorata* under varying environmental conditions. In addition to its promising reforestation potential (Wishnie et al. 2007), *T. rosea* can be grown with low technical inputs, which is aspired for sustainable agroforestry systems (Nair 1989).

Remarkably, none of the combinations of timber species with companion species revealed negative correlations in growth traits. Hence, no competitive interactions between companion and timber species were observed during the establishment phase of the trees. This finding gained under heterogeneous site conditions suggests that the association of the timber with the companion species investigated might be favorable under various site conditions.

Conclusions

The native timber species *Tabebuia rosea* has high potential for establishment on deforested land due to its high survival rate and good growth performance, in contrast to *Cedrela odorata*. *T. rosea* thus deserves further investigation as a promising species for different tree planting strategies. Stakeholders in Central and South America may be interested in verifying the expected high suitability of this species for use in reforestation as well as in agroforestry and silvopastoral systems, as it is available in the region and important for local and international timber markets.

Productivity of both *T. rosea* and *C. odorata* was not derogated by interspecific competition through the surrounding multipurpose species *Gliricidia sepium* or *Guazuma ulmifolia*. These native companion species expand the capacity of silvopastoral systems to satisfy a wider range of landholder needs, as they might improve pasture quality through reduced degradation, provide fuel wood and can be used as important supplemental feed during the dry season. Although *G. sepium* did not facilitate timber growth in the first 2 years after establishment, it might provide nitrogen to neighboring trees when tree individuals have fully established. Thus, the presented new planting design for silvopastoral reforestation systems may offer an additional economical benefit without reduced tree productivity or additional management effort.

This study documents that a crucial aspect to be considered to ensure productivity and profitability of tropical tree planting strategies is a careful selection of the timber species. Therefore, further investigations on reforestation potential of timber species, particularly little-known native species, are necessary to provide alternatives to the limited number of species currently used for targeted tree planting on deforested land.

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